THE UNIONACEA (MOLLUSCA, LAMELLIBRANCHIATA) OF SOUTH–CENTRAL AFRICA

By

C. C. APPLETON*

Bilharzia Field Research Unit, South African Medical Research Council, Nelspruit

(With 8 figures and 1 table)

ABSTRACT

Twelve species of the Unionacea (Mollusca, Lamellibranchiata), five Unionidae and six Mutelidae and one Etheriidae, are recorded from the south–central region of Africa. Their distribution within this region, which is taken to embrace the catchments of the Kunene, Cuvelai, Okavango, Linyanti and Zambezi River systems, is updated. Attention is drawn to the paucity of ecological data relevant to the freshwater bivalves of Africa and the detailed locality notes made by several collectors are therefore included.

CONTENTS

INTRODUCTION

Knowledge of the Unionacea of the southern central African region embracing the Kunene, Cuvelai, Okavango and Zambezi River systems (i.e. between latitudes 9° and 21°S) has hitherto been limited, particularly with regard to the Kunene and Okavango. During the past decade, however, a considerable amount of material has been collected from these drainages and through the co-operation of a number of individuals and institutions the author has been able to examine examples of eleven of the twelve recorded unionacean species, five Unionidae, five Mutelidae and one Etheriidae, per-mitting an updating of knowledge on the composition and distribution of this bivalve fauna. Unfortunately no material is available from the middle and lower Zambezi, east of Lake Kariba. However, the bivalve fauna of Lake MacIlwaine on the Hunyani River, a tributary to the middle Zambezi, has been discussed by Marshall (1975) and the malacofauna of Lake Malawi has been dealt with by Crowley *et al.* (1964) and Mandahl-Barth (1972). In addition, the bivalves of the adjacent Bangweulu–Luapala basin, the Congo River system, and Mozam-bique have been variously discussed by Mandahl-Barth (1968), Pilsbry &

* Present address:
    School of Environmental & Life Sciences, Murdoch University, Murdoch, Western Australia 6153.

Bequaert (1927), Azevedo *et al.* (1961), and Braga (1952). In the present contribution the systematic arrangement of Connolly (1939) has been followed, though changes in nomenclature made by Haas (1969), Mandahl-Barth (1968, 1972) and Heard & Vail (1976) have been incorporated.

Figure 1 shows the watercourses referred to in the text. These comprise both large, perennial rivers such as the Kunene and Okavango with volumes that may exceed 6 000 m³/s during high flood which can drop to less than 15 m³/s in dry years (Stengel 1963), as well as largely seasonal floodplain or deltaic environments such as the Okavango delta, Linyanti swamp, eastern Caprivi floodplain and the Etosha Pan.

Where measurements of shell height (altitude) are given, maximum height is used (except where indicated) in preference to umbonal height because in many cases the umbones were eroded to such an extent that considerable inaccuracies would have been introduced.

The following abbreviations are used:

> SAM   South African Museum, Cape Town
> NM   Natal Museum, Pietermaritzburg
> TM   Transvaal Museum, Pretoria
> MMK   McGregor Memorial Museum, Kimberley
> SMN   State Museum, Windhoek

Where no abbreviations are given, the material has been lodged in the collection of the South African Museum, Cape Town.
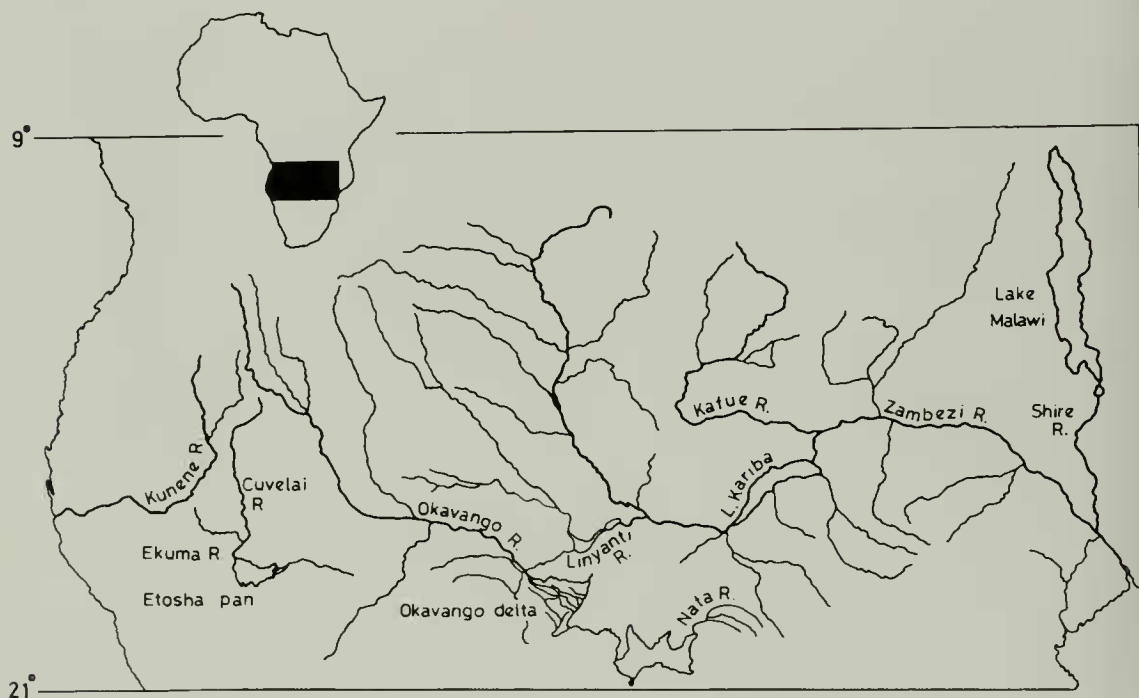

Fig. 1. Map of south–central Africa (between latitudes 9° and 21°S) showing the river systems referred to in the text.

SYSTEMATIC DISCUSSION

Superfamily UNIONACEA

Family **Unionidae**

Although many species of Unionidae have been described from southern Africa (south of but including the investigated area) only four are recognized here. These are *Unio caffer*, *Caelatura kunenensis*, *C. mossambicensis* and *C. framesi* and may even be too many. All except *C. framesi*, a southerly species, occur in the area under discussion.

Unio Retzius, 1788

Unio caffer Krauss, 1848

Fig. 2A

Material examined

Zambezi River system:

> Kafue River south of Itezhitezhi, Zambia. R. M. Derricourt leg. 1975, 2 specimens + 1 valve.
> Matopos, Rhodesia, M. N. Bruton leg. 1973, 3 specimens.
> Nyamandlelovu (on Gwaai River), Rhodesia. R. H. R. Stevenson leg. 26 May 1924, 1 specimen, NM–A5364.
> Victoria Falls, collector unknown, 1 valve, MMK MOL–328.
> Upper Zambezi River, G. C. Shortridge leg., 1 valve, MMK MOL–327.
> Hunyani River, Darwendale, B. E. Marshall leg. May 1975, 2 specimens + 1 valve.
> Gwenoro dam, Gwelo, Rhodesia. B. E. Marshall leg., 1 specimen.

Heard & Vail (1976) have discussed in detail the anatomy and systematic position of this species and have illustrated its hooked glochidium. These glochidia are considerably smaller than those of *Caelatura kunenensis* found by the present author. *Unio caffer*, which attains a far larger size than any other southern African unionid, is characterized by its heavy shell, strong cardinal and lateral teeth and downward-sloping hinge line. The posterodorsal ridge is usually pronounced though not sharp. Some zigzag sculpture is present on juvenile shells up to about 21 mm in length; on older shells this is generally worn away and only growth striae remain. Only the outer demibranchs are modified to form marsupia.

The records from the Kafue and upper Zambezi rivers are the most northerly for this southern African species. Marshall (1975) has reported it from Lake MacIlwaine (Rhodesia). It is, however, uncommon in the area under discussion and has not been recorded from the Okavango, Cuvelai or Kunene River systems, i.e. west of longitude 23°E.

A record of *U. caffer* from Amaramba in the Niassa district of Mozambique (Azevedo *et al.* 1961), consisting of a single juvenile approximately

6,1 × 3,6 × 2,2 mm, has been suggested by Oberholzer & Van Eeden (1967) to refer to a higher-shelled species, viz. *Caelatura mossambicensis*. This is probably correct since the Amaramba specimen has a L/H ratio of 1,70 whereas a juvenile *U. caffer* of similar size from the eastern Transvaal escarpment has a ratio of 1,95. No juvenile *C. mossambicensis* are available but comparable *C. kunenensis* from the Kafue River (NM–A5366) have L/H ratios of 1,58–1,62. Furthermore, the illustration by Azevedo *et al.* (1961) of sculpture round only the umbone is in agreement with the general paucity of sculpture found in *C. mossambicensis* and is in marked contrast to juvenile *U. caffer* where a sculpture pattern of two to three broken chevrons crosses the entire shell.

Unio is a palearctic genus whose distribution in Africa is, as Brown (1978) has pointed out, restricted to the cooler regions of the continent. There is thus a wide gap between the ranges of *U. caffer* in South Africa, South West Africa and Rhodesia and that of the nearest related species in North Africa.

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Caelatura Conrad, 1853

Caelatura kunenensis (Mousson, 1887)

Fig. 2B–C

</div>

Material examined

Kunene River system:

> Pump station, Huila (district), Angola, M. J. Penrith & J. Batista leg. 29 September 1972, 2 specimens, SMN–75540.
>
> Pool below Ruacana Falls, B. F. Kensley leg. 1972, 50 specimens + 11 valves.
>
> Ruacana Falls (17°23′S, 14°13′E), M.-L. Penrith leg. 1976, 10 specimens, SMN–75598.
>
> Great (Kambele) Falls (according to M. J. Penrith this is probably an old name for the minor cataracts about 10 km above Ruacana), K. H. Barnard leg. 1923, 2 valves, SAM–A6640 and A6647.
>
> 44 km west of Ondarusu Falls, M. J. Penrith leg. 23–25 October 1971, 1 specimen, SMN–75494.
>
> 72 km west of Ondarusu Falls, M. J. Penrith leg. 28 October 1971, 1 specimen, SMN–75494.
>
> Kunene River at Otjinungua, W. D. Haacke leg. May 1966, 2 specimens, TM–9334 and 9335.

Cuvelai/Etosha system:

> Ekuma floodplain, Etosha Pan National Park, K. L. Tinley leg. 27 December 1965, 1 specimen, NM–A5369.

Okavango River system:

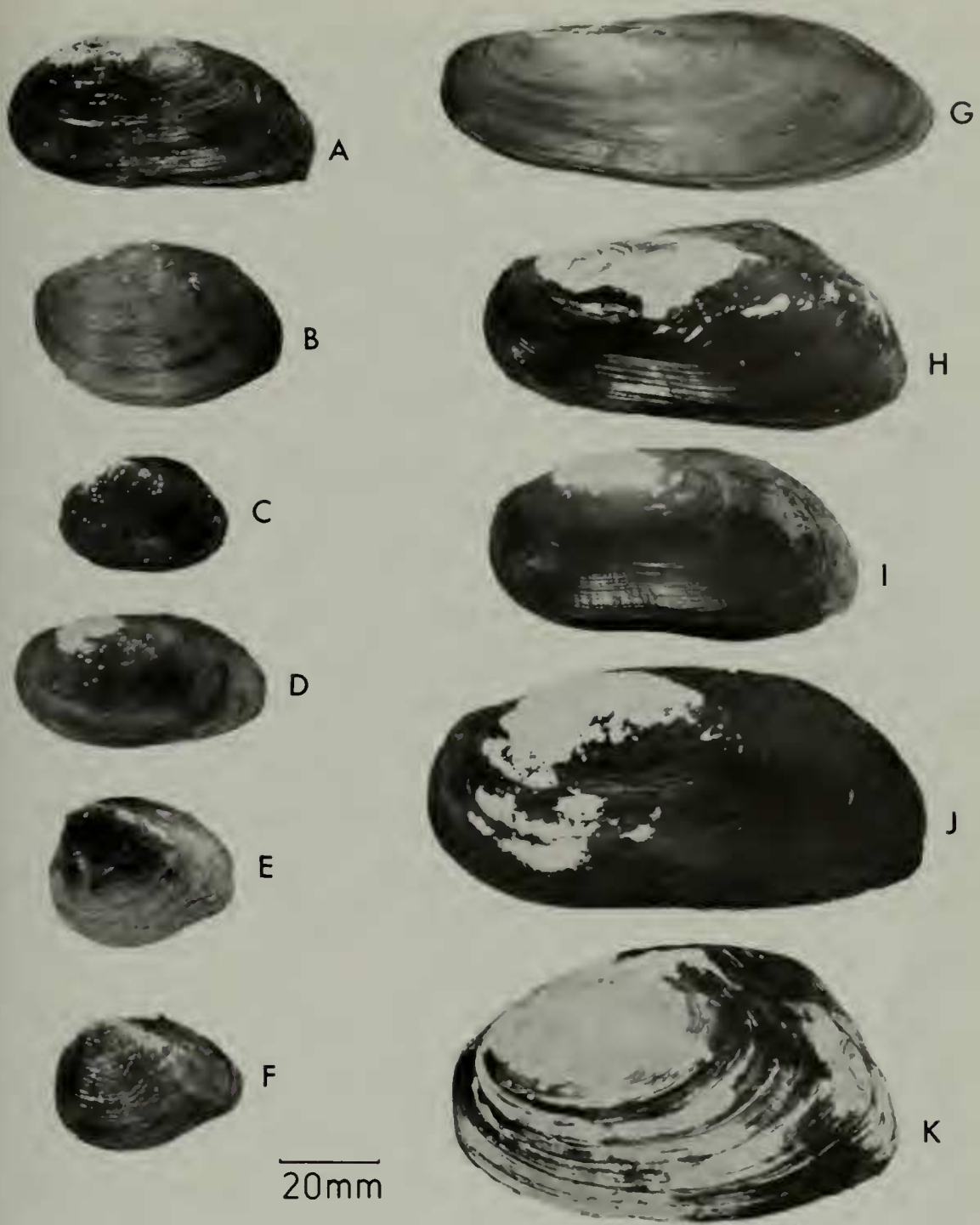> Okavango River, G. C. Shortridge leg., 5 specimens, NM–3999; 3 specimens, TM–38541.

Fig. 2. Left valves of ten species of Unionacea from south–central Africa.

A. *Unio caffer* Krauss, 1848, Kafue River south of Itezhitezhi, Zambia. 62,5 × 31,9 mm.
B. *Caelatura kunenensis* (Mousson, 1887), 'typical form', Thamalakane River in Okavango delta, Botswana. 50,2 × 33,2 mm. C. *Caelatura kunenensis* (Mousson, 1887), 'Zambezi form', Kalala Island in Kafue River, Zambia. 33,8 × 23,4 mm. D. *Caelatura mossambicensis* (Martens, 1859), eastern end of Lake Kariba, Rhodesia. 50,8 × 27,0 mm. E. *Caelatura nyassaensis* (Lea, 1964), off Nkopola, Lake Malawi, Malawi. 37,6 × 31,0 mm. F. *Caelatura hypsiprymna* (von Martens, 1897), off Nkopola, Lake Malawi, Malawi. 37,3 × 28,3 mm. G. *Mutela dubia* (Gmelin, 1793). Thamalakane River in Okavango delta, Botswana. 101,3 × 36,1 mm. H. *Mutela alata* (Lea, 1864). Lake Malawi, 87,7 × 41,0 mm. I. *Aspatharia* (*Aspatharia*) *pfeifferiana* (Bernardi, 1860), upper Zambezi River, Zambia. 78,3 × 38,0 mm. J. *Aspatharia* (*Spathopsis*) *wahlbergi* (Krauss, 1848), eastern end of Lake Kariba, Rhodesia. 102,5 × 49,2 mm. K. *Aspatharia* (*Spathopsis*) *nyassaensis* (Lea, 1864), Lake Malawi, Malawi. 91,5 × 56,4 mm.

Omuramba Omataka, G. C. Shortridge leg., 22 specimens, MMK
    MOL–327. Label reads: 'everything collected in dry annually flooded
    bed of Omuramba Omataka at or within 15 miles (23 km) of junction
    with Okavango'. (The Omuramba Omataka is the largest, albeit
    seasonal, watercourse flowing from South West Africa to the Okavango
    River.)

Thamalakane River at Maun, Okavango delta, collector unknown, 20 May
    1930, 181 specimens + 14 valves, TM–5565; same locality, P. A.
    Reavell leg. 1973; 147 specimens.

Rakops on the Botletle River between the Okavango delta and the Makari-
    kari Pan, collector unknown, 3 specimens.

Chobe/Linyanti River system:

Luapala Island in Linyanti swamp, 17°22'S 23°42'E 'from shallow sand-
    bank, water level dropped'. B. van der Waal leg. 1975, 1 specimen
    + 2 valves.

Zambezi River system:

'Zambezi', 1 specimen + 1 valve, NM–3371.

'Zambezi', B. E. Marshall don., 4 specimens.

Zambezi at Mongu Lealui, Barotse Valley, Zambia, 5 specimens + 1 valve,
    NM–4000. Type locality of *Nodularia croninae*, synonym of
    C. kunenensis.

Upper Zambezi River, G. C. Shortridge leg., 2 specimens + 21 valves,
    MMK MOL–327.

Zambezi at Katima Mulilo, eastern Caprivi, W. D. Haacke leg. May 1966,
    TM–11009; same locality, B. van der Waal leg. 1975, 3 specimens;
    R. J. Pitchford leg. 1976, 2 valves.

Victoria Falls, K. H. Barnard leg. 1946, 2 specimens + 1 valve.

Kafue River, Kalala Island Rest Camp, Kafue National Park, Zambia,
    A. C. van Bruggen leg. 2–3 November 1966, 3 specimens + 8 valves,
    'ex flood debris of Kafue River', NM–A5366.

Kalala Island in Kafue River, Zambia, R. M. Derricourt leg. 1975, 26 speci-
    mens + 8 valves.

Itezhitezhi area of Kafue River, Zambia, R. M. Derricourt leg. 1975,
    10 specimens + 5 valves.

Although Haas (1936, 1969) included *Unio zambeziensis* Preston and *Nodu-
laria croninae* Walker from the Zambezi River system in the synonymy of this
species, two distinct forms are nevertheless recognizable, at least in adult shells.
A generally small, robust form, dark brown in colour and usually with zigzag
sculpture over most of the shell, corresponding to *Unio zambeziensis* (hereafter
referred to as the Zambezi form) from the Victoria Falls is also known from
the northern tributaries of the Zambezi as well as the Kunene River. A larger
though more compressed form, with a lower length/height ratio, light brown

in the adult stage and with sculpture over much of the shell, occurs in the Okavango River and its delta, and in the Linyanti swamp. This latter form, according to Mandahl-Barth (*in litt*. 13 October 1976), corresponds to typical *C. kunenensis*. An apparently intermediate form occurs in the Zambezi River at Katima Mulilo, the Okavango River and Ekuma floodplain. Shells referable to *Nodularia croninae* are known from the upper reaches of the Zambezi in eastern Zambia. Figure 3 shows a significant difference ($p < 0,01$) between the shapes (as indicated by L/H v. length) of the Zambezi form and typical *C. kunenensis*, particularly amongst larger specimens. There is no meaningful difference in shell width relative to length and these dimensions are not shown. The measurements given by Dartevelle (1939) for five specimens of *C. kunenensis* from the upper Kunene (no precise locality given) indicate that these should belong to the typical form.

Juveniles up to approximately 34×23 mm may be sculptured over the whole shell surface. In larger shells the sculpturing persists posteriorly and anteriorly, although specimens corresponding to *N. croninae* are generally smoother than the more southerly forms. Juveniles of the Zambezi form are usually green-yellow. The very small valves from the Kafue River (NM–A5366) are dominated by rugose and sometimes lamellate zigzag sculpture over the whole shell surface.

Nothing is known of the nature of the localities where shells corresponding to *N. croninae* were found, but the Zambezi form and typical *C. kunenensis* may represent adaptations to fundamentally different environmental conditions. The present data indicate that the former occurs in lotic environments (perennial, flowing rivers) whereas the latter is found in lentic and often seasonally inundated areas. G. Mandahl-Barth has suggested (*in litt*. 13 October 1976) that the Zambezi form may, in fact, be a subspecies of *C. kunenensis*. *Caelatura*
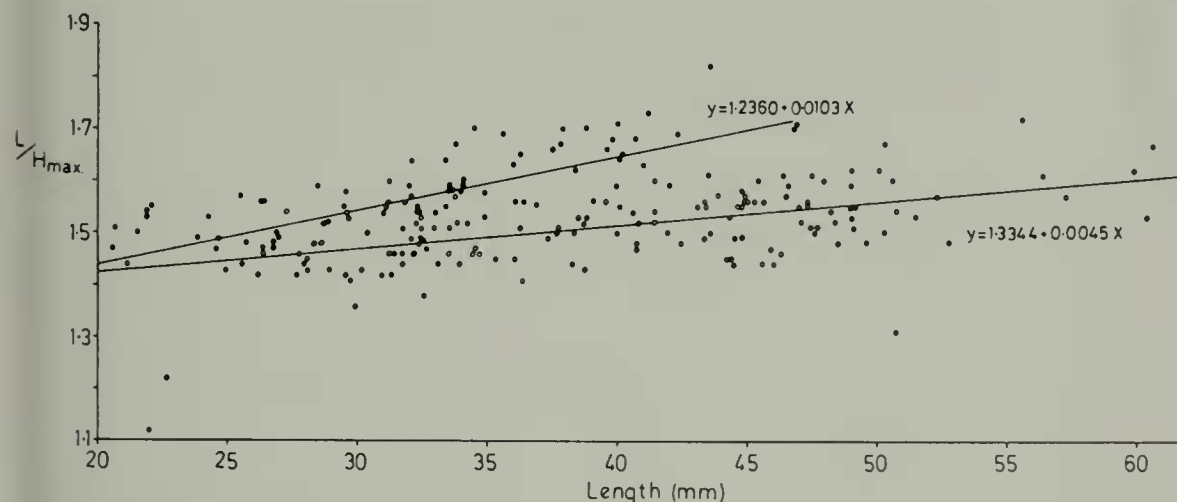

Fig. 3. *Caelatura kunenensis*: relationship between L/H and length of river (Ruacana Falls, Kunene River, n = 71) and swamp (Thamalakane River, Okavango delta, n = 145) forms as shown by linear regression lines fitted by the method of least squares. Solid circles = Kunene River; open circles = Okavango delta.

kunenensis is thus a western species confined to the Kunene and Okavango River systems as well as the upper Zambezi and its tributaries (Kafue, Luapala and Linyanti) as far north as approximately 11°S latitude. The 'typical' form seems allied to *Caelatura choziensis* (Preston) from Lake Bangweulu and the Chambeshi River as illustrated by Haas (1936) and Mandahl-Barth (1972).

Although the gonads were not examined histologically, dissection of a series of specimens from below the Ruacana Falls in the Kunene River showed that 58 per cent (25/43) were functional females with all four demibranchs modified to marsupia. The remaining 42 per cent (18/43) bore no sign of marsupia and were considered males. The smallest female measured 25,6 × 17,8 × 12,0 mm. Although most marsupia were charged with embryos some contained sub-oval glochidia. The uniformly punctate valves of these glochidia were virtually equal in length and height (Fig. 4); the mean dimensions of six examples were 0,263 × 0,265 mm. No hooks were seen, although the glochidia may not have been fully developed.
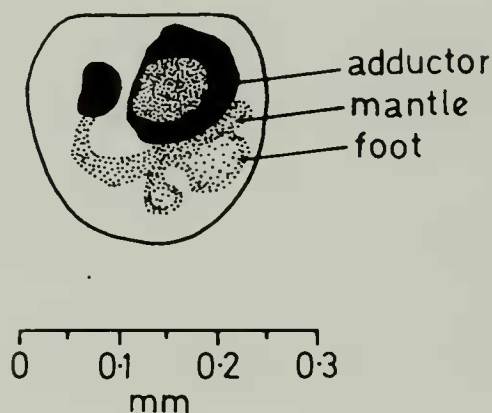
Fig. 4. Camera lucida drawing of a glochidium from an outer demibranch of *Caelatura kunenensis* (38,6 × 23,2 × 17,6 mm) from Ruacana Falls, Kunene River.

Small leeches, *Batracobdella tricarinata* (Blanchard) were found in the pallial cavities of 16,3 per cent (7/43) of *Caelatura kunenensis* from Ruacana on the Kunene River and a single emphemeropteran nymph (Baetidae: *Centroptiloides?* sp.) was present in the pallial cavity of a specimen from the Zambezi at Katima Mulilo. Although this nymph is unlikely to be a 'pallial cavity' dweller, *Centroptiloides* nymphs are unusual among mayflies in being predaceous (F. M. Chutter, *in litt.* 31 January 1977). The presence of insect larvae inside bivalves was also noted by Beedham (1971) who found chironomid larvae between the mantle and shell of *Anodonta cygnea* (Linnaeus) (Unionidae) in England. Woodward (1974) recorded numerous examples of a hydracarine (though not a parasitic stage) within the pallial cavity of *Caelatura* cf. *aegyptica* (Cailliaud) from Lake Chad.

Caelatura mossambicensis (von Martens, 1860)

Fig. 2D

Material examined

Zambezi River system:

> Eastern end of Lake Kariba in Nyanyana River estuary, Sanyati basin, 5–7 m in soft sand/silt, D. H. S. Kenmuir leg. 17 December 1976, 49 specimens.
>
> Lake MacIlwaine (on Hunyani River, tributary to Zambezi), B. E. Marshall leg., 14 specimens + 14 valves.
>
> Hunyani River at Darwendale, Rhodesia (below Lake McIlwaine), B. E. Marshall leg., 3 specimens.

This species may be distinguished from *Caelatura kunenensis* by being relatively longer and more compressed, and by having a thinner shell with poorly developed sculpture. In order to demonstrate the differences between the shell width v. length ratio of *C. mossambicensis* and *C. kunenensis*, the Lake Kariba *mossambicensis* were compared statistically to *kunenensis* from three other localities, the Kafue River, Kunene River and Okavango delta. Linear regression lines were fitted to each of the four sets of data by the method of least squares and their slopes (not shown) compared in a pairwise manner (Table 1). This showed that the shell width v. length ratio of all the *C. kunenensis* populations differed significantly from *C. mossambicensis*, whereas there was no significant difference between any of the individual *C. kunenensis* populations. The three sets of data for *C. kunenensis* were then pooled and compared with *C. mossambicensis* from Lake Kariba (Fig. 5). This showed a significant difference ($p < 0,001$) between the shell width v. length ratio for the two species.

TABLE 1

Pairwise comparisons between (A) *Caelatura mossambicensis* from Lake Kariba and (B) *C. kunenensis* from the Kafue and Kunene rivers and the Okavango delta, using the slopes of individual regression lines for shell width v. length.

A. Comparison between *C. mossambicensis* and *C. kunenensis*

C. mossambicensis	*C. kunenensis*	t	degrees of freedom	significance
Lake Kariba	Kafue River	2,1400	68	*
Lake Kariba	Kunene River	3,1318	108	**
Lake Kariba	Okavango delta	3,7227	191	***
Lake Kariba	three above localities combined	19,5344	279	***

B. Comparison between three geographically different populations of *C. kunenensis*

Localities		t	degrees of freedom	significance
Kafue River	Kunene River	1,0691	84	ns
Kafue River	Okavango delta	1,0069	167	ns
Kunene River	Okavango delta	0,1677	207	ns

* = significant at 5 % level
** = significant at 1 % level
*** = significant at 0,1 % level
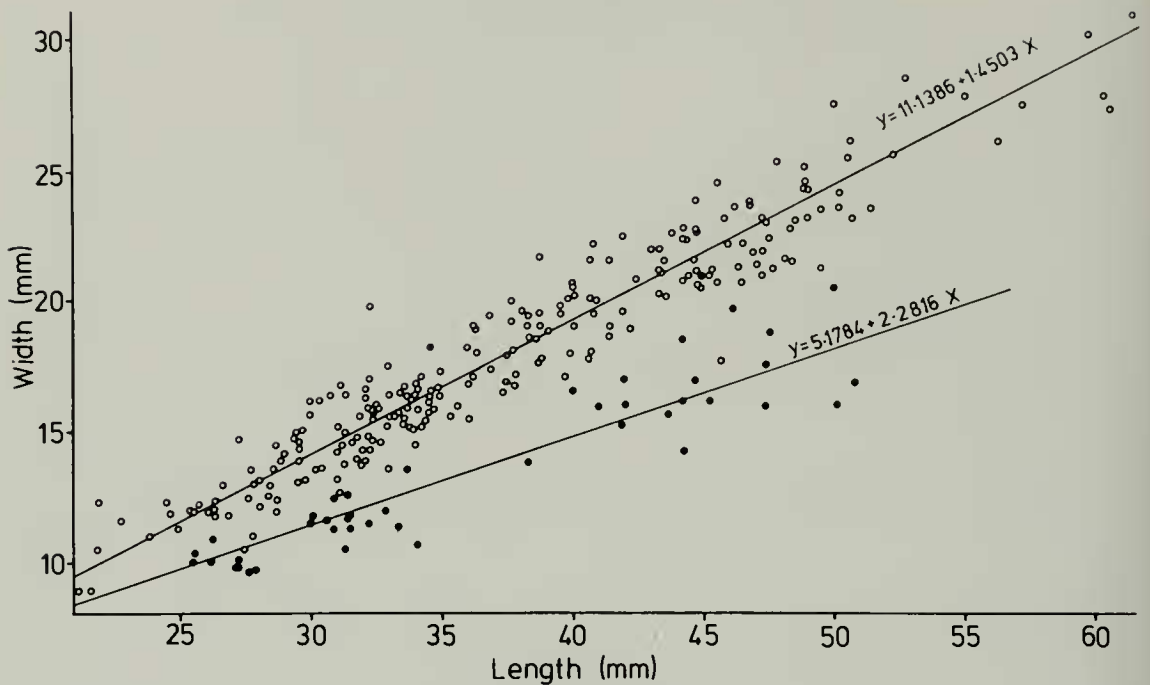ns = not significant

Fig. 5. Diagram relating shell width to shell length for *Caelatura kunenensis* (open circles) and *Caelatura mossanbicensis* (solid circles) by means of linear regression lines fitted by the method of least squares.

Juvenile *C. mossambicensis* show zigzag sculpture anterior and posterior to the umbones, but in adults only a little remains visible. The colour of the periostracum varies from green-brown to uniform dark brown while juveniles may be light brown to greenish. Teeth are much weaker and less projecting than in *C. kunenensis*.

The type locality of *C. mossambicensis* is Tete on the lower Zambezi. It has also been recorded near Chemba (Germain 1935) and Mazarra (Azevedo *et al.* 1961; Connolly 1939) and in Lake MacIlwaine on the Hunyani River, Rhodesia (Marshall 1975). In addition, it has been collected from Lake Malawi, its tributary the South Rukuru River, and the Shire River which connects the lake to the Zambezi (Mandahl-Barth 1972). *Caelatura mossambicensis* is closely allied to *Caelatura framesi* (Connolly 1925*b*) from further south (Brown 1967; Appleton 1977), and Mandahl-Barth (*in litt.* 14 December 1976) is of the opinion that *C. framesi* is merely a southerly form of *C. mossambicensis*. The distribution of these two 'species' abut one another in central Mozambique. *Caelatura mossambicensis* thus appears to be an eastern species confined to the coastal peneplain of east and south-east Africa from the Kingani River near Bagamoyo in Tanzania (about 6°25′S) (Haas 1962) to the Pongola River floodplain (about 27°00′S) in north-eastern Natal (Appleton 1977; Brown 1967; Pretorius *et al.* 1975), and penetrating the Zambezi River system as far as Lakes Kariba and Malawi.

Caelatura nyassaensis (Lea, 1864)

Fig. 2E

Material examined

   Monkey Bay, Lake Malawi, M. N. Bruton leg. March 1973, 1 specimen;
      alive in sandy mud at about 3 m, C. C. Appleton & D. H. Eccles leg.
      September 1976, 4 specimens.
   Off Nkopola, Lake Malawi, alive in sand about 3 m, C. C. Appleton leg.
      September 1976, 3 specimens + 1 valve.

A small, squat shell with very little or no sculpture, ventral margin curved
downward posteriorly and sharp umbonal ridge. The L/H ratio of the specimens
examined ranged from 1,24 to 1,40 (mean 1,32).

Caelatura hypsiprymna (von Martens, 1897)

Fig. 2F

Material examined

   Monkey Bay, Lake Malawi, B. Boswell leg., 3 specimens + 1 valve,
      TM–11239; alive in sandy mud at about 3 m, C. C. Appleton &
      D. H. Eccles leg. September 1976, 4 specimens.
   Off Nkopola, Lake Malawi, alive in sand about 3 m, C. C. Appleton leg.
      September 1976, 8 specimens + 2 valves.

Another small, squat species with more chevron sculpture than *C. nyassa-
ensis*. This sculpture sometimes extends over most of the shell and is particularly
evident in smaller individuals which, as Mandahl-Barth (1972) has pointed out,
bear a close resemblance to the Zambezi form of *C. kunenensis*. The umbonal
ridge of *C. hypsiprymna* is pronounced though not sharp and the shell tends
to be rather attenuated posteroventrally. The L/H ratios of those examined
range from 1,13 to 1,53 (mean 1,34).

These two species appear to be endemic to Lake Malawi and have been
recorded from many localities in the lake and Shire River at Mangoche to
depths of 12,2 m (*C. nyassaensis*) and 79,3 m (*C. hypsiprymna*) (Crowley *et al.*
1964; Mandahl-Barth 1972). Mandahl-Barth (1972) gives a good description
of the differences between these species. To this it may be added that their
L/H ratios are lower than those of other Caelaturae of south-central Africa.

Family **Mutelidae**

Mutela Scopoli, 1777

Mutela dubia (Gmelin, 1793)

Fig. 2G

Material examined

Kunene River system:

   Pool below Ruacana Falls, B. F. Kensley leg. 1973, 4 specimens.

Okavango River system:

Okavango River, S.W.A., G. C. Shortridge leg. 5 specimens, NM–3912; 3 specimens + 1 valve, MMK MOL–336.

Thamalakane River at Maun, Okavango delta, donor unknown, 2 specimens, TM–1075; P. A. Reavell leg. 1973, 42 specimens.

Chobe/Linyanti River system:

Lupala Island in Linyanti swamp, 17°22′S 23°42′E, 'from shallow sandbank, water level dropped'. B. van der Waal leg. 1973, 7 specimens.

Mutualutze Lusese, a large permanent channel or 'mulapo' in eastern Caprivi floodplain, 17°45′S 24°44′E. B. van der Waal leg. 1973, 1 specimen.

Zambezi River system:

Zambezi at Mongu Lealui, Barotse Valley, Zambia, Mrs. T. H. Howard leg., 1 specimen, NM–3914.

Upper Zambezi, G. C. Shortridge leg., 1 specimen, MMK MOL–336.

Zambezi at Katimo Mulilo, B. van der Waal leg. 1975, 1 specimen.

Eastern end of Lake Kariba, Nyanana estuary in Sanyati basin, 5–7 m in soft sand/silt, D. H. S. Kenmuir leg. 17 December 1976, 8 specimens.

Connolly (1939) identified *Mutela mabilli* (Rochebrune) from the Okavango River but Haas (1936), after examining the same material, recorded it as *M. nilotica mabilli*, a southern race of the north African *M. nilotica*. Later, however, Haas (1969) placed *M. mabilli* into synonymy with the west African *M. dubia*. Although the present material varies considerably in shape from almost triangular to lanceolate, the majority of shells do, in fact, correspond well to *M. dubia* as illustrated by Pilsbry & Bequaert (1927).

Both thin and thick (robust) shelled forms may occur in the same locality, but the former appears to be the most common. The thick-shelled form from the Okavango delta is on average 4,9 g heavier than the thin-shelled form of similar length, and has a rather distinct shape (Fig. 6).

Mutela dubia is a west African species which reaches the southernmost limits of its distribution in the Kunene, Okavango and Zambezi systems. The only other record of *M. dubia* from the Kunene is a brief reference to this species from the upper Kunene by Dartevelle (1939). The accuracy of the record of *Mutela rostrata* (Rang) (now included in the synonymy of *M. dubia* by Haas (1936, 1969)) from Lourenço Marques (Maputo) was questioned by Connolly (1925a, 1939) and to the present author's knowledge it remains the only record of *Mutela* from Mozambique south of the Zambezi River. Small leeches, *Batracobdella tricarinata* (Blanchard) (Branchiobdellidae), were found in the mantle cavities, notably around the palps, of two Ruacana (Kunene) specimens. The decimation of the littoral *M. dubia* population of Lake McIlwaine (Rhodesia) after a drop in water level (Marshall, 1975, 1978) may have been due in part at least to the natural gape of the valves of this species reducing the species' resistance to dessication.
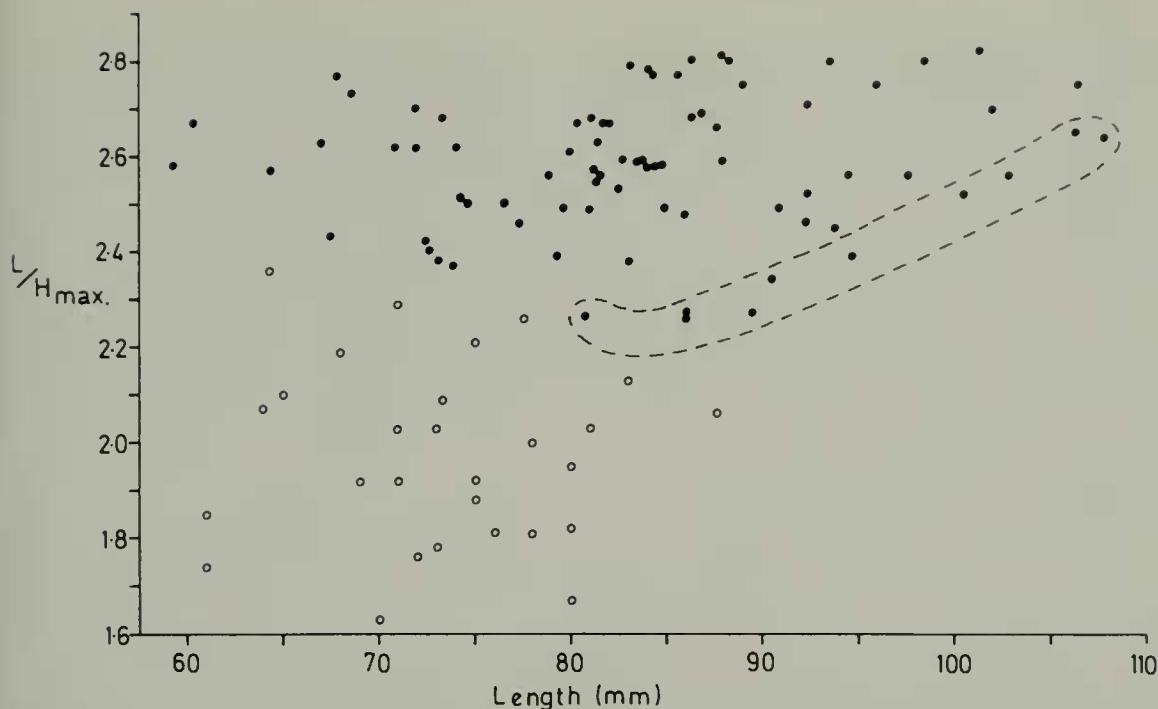
Fig. 6. *Mutela dubia:* scatter diagram relating L/H $_{max}$ to valve length. The dotted line indicates the robust form which constituted 22,3 per cent of *M. dubia* from the Okavango delta. Solid triangles = Zambezi River; open triangles = eastern Caprivi/Linyanti floodplain; solid circles = Okavango River system; open circles = Kunene River.

Mutela alata (Lea, 1864)

Fig. 2H

Material examined

Monkey Bay, Lake Malawi, M. N. Bruton leg. March 1973, 3 specimens; C. C. Appleton leg. September 1976, 1 specimen.

Known from a variety of localities in Lake Malawi and the Shire River to a depth of 27,5 m (Crowley *et al.* 1964; Mandahl-Barth 1972). Both thin- and thick-shelled forms occur amongst the material available. *Mutela alata* is characterized, as its name implies, by its high (alate) posterodorsal 'wing', though this is not as high as that of *Mutela hargeri* (Smith) from Lake Mweru (Zambia). The L/H ratio (2,06–2,36) tends to be lower than for *M. dubia* (2,26–2,82) (Fig. 6).

This species is apparently endemic to Lake Malawi and the Shire River although Mandahl-Barth (1972) considered that it is related to *M. hargeri* and (*in litt.* 2 February 1977) to the widely distributed *dubia–nilotica–mabilli* group.

Aspatharia Bourguignat, 1885

Representatives of two subgenera, *Aspatharia* s.s. and *Spathopsis*, occur in southern central Africa and may be distinguished by the character of the inhalent opening into the branchial chamber. In *Aspatharia* s.s. there is a distinct inhalent aperture formed by a fusion of the mantle edges, while in *Aspatharia* (*Spathopsis*) there is no such fusion and the mantle margins thus

remain free below the exhalent aperture (Fig. 7). In this respect *Aspatharia* s.s. is unique among the southern and central African Unionacea.
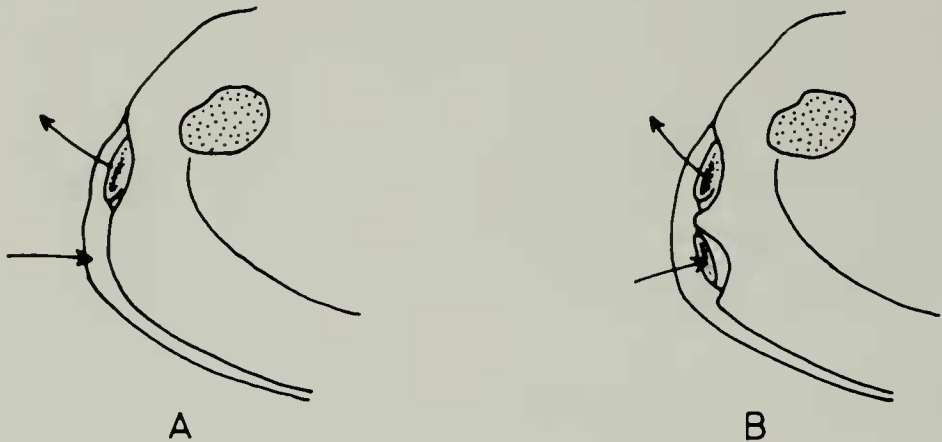

Fig. 7. Digrammatic illustration comparing the inhalent apertures of *Aspatharia* (*Aspatharia*) and *Aspatharia* (*Spathopsis*). A. *Aspatharia* s.s. lacks a discrete aperture and the inhalent current is simply drawn between the mantle edges into the branchial chamber. B. *Aspatharia* (*Spathopsis*) possesses a distinct inhalent aperture through which the current enters the branchial chamber.

Aspatharia (*Aspatharia*) *pfeifferiana* (Bernardi, 1860)

Fig. 2I

Material examined

Kunene River system:

Pool below Ruacana Falls, B. F. Kensley leg. 1973, 1 specimen.

Ontoruthu Falls (= Ondorusu Falls, 17°24'S 13°57'E), B. F. Kensley leg. 1972, 4 specimens + 2 valves.

Otjinungua, Kaokoveld, W. D. Haacke leg. May 1966, 1 specimen, TM–9335.

Okavango River system:

Okavango River, South West Africa, G. C. Shortridge leg., 6 specimens, NM–3913.

Omuramba Omataka, G. C. Shortridge leg., 7 specimens, MMK MOL–334.

Boro River, Okavango delta, P. A. Reavell leg. 1973, 3 specimens + 5 valves.

Zambezi River system:

Upper Zambezi Valley, G. C. Shortridge leg., 7 specimens, MMK MOL–334.

Sandbank in Zambezi at Katima Mulilo, B. van der Waal leg. 1974, 1 specimen.

Itezhitezhi area of Kafue River, Zambia, R. M. Derricourt leg. 1975, 1 specimen + 3 valves.

Records of this smallish species from the Kunene River at Fort Roçados in southern Angola, the Okavango River in Owambo, and the Hunyani River (a tributary of the Zambezi) in Rhodesia were cited by Haas (1936).

Adpatharia pfeifferiana is a predominantly west African species reaching the southern limits of its range in this area. In several localities it was found together with *A. (Spathopsis) wahlbergi* from which it may be distinguished by its concave ventral margin and much smaller pedal protractor muscle scar. Empty shells of *A. pfeifferiana* can usually be distinguished from those of *A. wahlbergi* as shown in Figure 8. This relates the L/H $_{(ad\ umbone)}$ ratio to
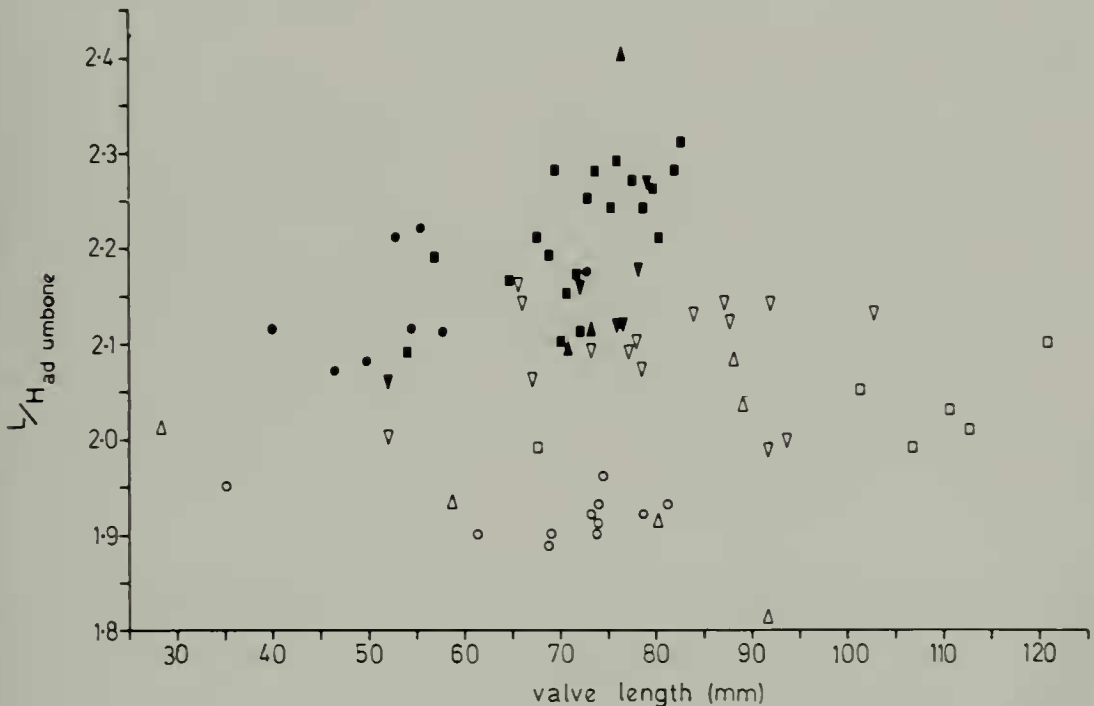

Fig. 8. Scatter diagrams relating the L/H $_{ad\ umbone}$ ratio to valve length for *Aspatharia (A.) pfeifferiana* (solid symbols) and *Aspatharia (S.) wahlbergi* (open symbols). Circles = Kunene River; triangles = Kafue River; inverted triangles = Zambezi River system; squares = Okavango River system.

valve length; umbonal height is used despite shell erosion in order to take into account the marked concavity of the ventral margin (below the umbonal area) typical of *A. pfeifferiana*.

The only other member of *Aspatharia* s.s. recorded from south-central Africa is *A. (A.) subreniformis* (Sowerby) from Lake Malawi and the Shire River. Mandahl-Barth (1972) doubts that this represents a valid species endemic to the lake and has suggested that it may be closely related to *A. (A.) pfeifferiana* (Bernardi) (= *A. rugifera* (Dunker) *fide* Haas 1969).

Aspatharia (*Spathopsis*) *wahlbergi* (Krauss, 1848)

Fig. 2J

Material examined

Kunene River system:

> Ruacana Falls, M. L. Penrith leg. 1973, 6 specimens, SMN–75597.
> Pool below Ruacana Falls, B. F. Kensley leg. 1973, 4 specimens + 1 valve.

Okavango River system:

> Nata River valley, between Maitengwe and Nata Police Station, Central district Botswana, donor unknown, 3 specimens + 4 valves, TM–11237.

Zambezi River system:

> Eastern end of Lake Kariba, Nyanana estuary in Sanyati basin, 5–7 m in soft sand/silt, D. H. S. Kenmuir leg. 17 December 1976, 13 specimens.
> Battlefields (on Sanyati River), Rhodesia, F. B. Parkinson leg., 1 specimen, NM–2703; 1 specimen, NMK MOL–335.
> Kalala Rest Camp, Kafue National Park, Zambia, 'ex flood debris of Kafue River', A. C. v. Bruggen leg. 2–3 November 1963, 1 valve, NM–A5365.
> Itezhitezhi area of Kafue River, Zambia, R. M. Derricourt leg. 1975, 1 specimen + 3 valves.
> Monkey Bay, Lake Malawi, B. Boswell leg. July 1968, 2 specimens, TM–11238.

Juveniles may display up to thirteen irregular riblets on the posterodorsal surface of the shell. They generally have a light-brown periostracum, but this darkens with age and adult specimens are dark brown to black. *A. wahlbergi* is also known from Mupa on the Cuvelai River, southern Angola (Haas 1936). This large species is widely distributed in central and east Africa from the Kunene River in the west to Mozambique in the east and thence southwards to the Transvaal and Zululand. Except for a single high-shelled juvenile from the confluence of Omuramba Omataka and Okavango rivers (Connolly 1931), and several specimens from the Nata River which flows into the Makarikari pan, *A. wahlbergi* has not been collected from the Okavango River system. Connolly's (1931) description of the singleton from South West Africa (L/H 1,71) is reminiscent of the Kunene River specimens whose L/H ratios (1,75–1,86, mean 1,82) are low for the species and which probably correspond to the variety *moutai* described by Dartevelle (1939) from the upper Kunene. The Nata River shells are much larger (to 120,9 × 62,1 mm, mean L/H 1,91), resembling those from the Limpopo River system whose drainage abuts on that of the Nata River. *A. wahlbergi* was not recorded from Lake Malawi itself by either Crowley *et al.* (1964) or Mandahl-Barth (1972) and its occurrence here is regarded as doubtful. Commenting on this, the latter author noted the species' presence in a roadside pool 5 km south of Monkey Bay. The shells (empty)

collected by Boswell (TM–11238) may have originated from a similar water body in the vicinity of Monkey Bay.

Braga (1952) illustrated a rather attenuated shell from Lagoa Bamba, Chibuto, Mozambique (L/H 2,36) which, although he gave no width measurement, appears otherwise comparable with the unusually obese specimens collected from Lagoa Pavi near Inhambane (MMK MOL–335) by H. A. Junod (L/H 2,13–2.21, mean 2,19) (not the same as those, also collected by Junod from Lagoa Pavi, recorded by Connolly 1925a). These shells may represent a lacustrine form occurring in the freshwater coastal lakes of the Mozambique peneplain.

The leech *Batracobdella tricarinata* (Blanchard) (Branchiobdellidae) was found in the mantle cavities of two specimens from Ruacana in the Kunene River.

Aspatharia (*Spathopsis*) *nyassaensis* (Lea, 1864)

Fig. 2K

Material examined

'Lake Malawi', donor unknown, 1 specimen NM–A5367.

Mangoche (Fort Johnston) on Shire River between Lakes Malawi and Malombe, K. Fuller leg. 19 November 1971, 1 specimen.

Monkey Bay, Lake Malawi, M. N. Bruton leg. March 1973, 1 specimen; C. C. Appleton & D. H. Eccles leg. September 1976, live in sandy mud at about 3 m, 1 specimen.

An unmistakable large, thick-shelled species which is endemic to Lake Malawi and the Shire River (Mandahl-Barth 1972). It is much higher posteriorly than the other large *Aspatharia*, *A. wahlbergi*, and the specimens to hand have a lower L/H $_{ad\ umbone}$ ratio of 1,70–1,96.

Aspatharia (*Spathopsis*) *petersi* (von Martens, 1859)

Although no specimens of this small, slender species are available from the area under discussion, Haas (1936) collected it from the Hunyani River 20 km south of Salisbury, Rhodesia. Connolly (1939) cites a record from Tete (the type locality) which lies on the lower Zambezi. *A. petersi* may be distinguished from *A. wahlbergi* by its much longer and narrower shell and hence its high L/H ratio of between 2,2 and 2,6 as opposed to 1,8 and 2,1 of the latter.

The distribution of this species is not well documented but it appears to be confined to the lower Zambezi as well as the eastwards flowing rivers of south-eastern Africa to about latitude 27°21'S. Specimens collected by B. Davies (Rhodes University) from Lake Tchal on the Incomati floodplain in Mozambique are, like *A. wahlbergi* from lakes in this region, longer in relation to height (L/H 2,30–2,57, mean 2,46) and more compressed than their counterparts from riverine environments. Data to hand suggest that the L/H ratios of shells from rivers range from 2,19 to 2,41 (mean 2,28).

Family **Etheriidae**

Etheria Lamarck, 1807

Etheria elliptica Lamarck, 1807

Material examined

Kunene River:

>   Kunene River at Otjinungua, Kaokoveld, W. D. Haacke leg. May 1966,
>   1 specimen + 2 valves, TM–93332.
>   Ontoruthu Falls (= Ondorusu Falls, 17°24′S 13°57′E), B. Kensley leg.
>   1973, 9 valves.

Yonge (1962) has discussed in detail the anatomy, evolution and life history of *Etheria elliptica* and concurs (Yonge 1962, 1978) with Haas (1969) and Thiele (1935) that *E. elliptica* is closely related to two other monotypic genera, the Colombian *Acostaea* and the Indian *Pseudomulleria*, and that these three comprise the family Etheriidae. The largest lower valve encountered measured 99,2 × 49,0 mm and the largest upper valve, 119,2 × 82,4 mm. One of the twelve upper valves available has the tube-like outgrowths (costae) typical of *E. elliptica* f. *tubifera* Sowerby. The only other record of *E. elliptica* from the Kunene River is by Germain in 1925 (cited by Haas 1936).

Only empty valves are available but M. J. Penrith (State Museum, Windhoek) has seen live specimens. He notes (*in litt.* 11 October 1976) that *E. elliptica* is very common in the Kunene from below the Ruacana Falls to the Foz du Cunene, where the last outcrops of rock occur (7 km from the mouth), and that it is usually found on the large boulders which in places form either banks or rapids in the river. However, it does not occur where flow is very fast, i.e. the shallower and narrower rapids. At the Ontorusu Falls the highest living animals were only a few centimetres below normal low water. He doubts whether the species occurs upstream of Ruacana and, if not, it would possess a distribution pattern which parallels that of some fish species. Dartevelle (1939) did not record *E. elliptica* from the upper Kunene.

Yonge (1962) noted that *E. elliptica* could be cemented to the substrate by either valve and that this occurred relatively late in its growth. The equivalve post-larva probably became attached (in the vertical position) initially by a byssus enabling it to withstand the high current velocities in which the adults are usually found. The later adoption of a horizontal posture was followed by cementation and growth as an inequivalve.

E. elliptica is widely distributed in tropical Africa and the Kunene shells represent its southernmost known locality.

DISCUSSION

Virtually nothing is known of the ecology of the freshwater bivalves of south–central Africa nor, indeed, of Africa generally. This is despite the fact that, although poor in numbers of species, the Unionacea of the river systems

under discussion are among the largest members of the benthos. Indeed, they may attain high population densities and may therefore constitute an important proportion of the benthic biomass. Relevant ecological studies include those of Pilsbry & Bequaert (1927) on the general malacology of the Congo River system, Fryer (1959, 1961) on the life-cycle of *Mutela bourguignati* (Ancey) in Lake Victoria, Marshall (1975) on the composition and distribution of the Unionacea of Lake MacIlwaine in Rhodesia, and Yonge (1962, 1978) on the settlement and cementation of *Etheria elliptica*. It is thus useful here to quote in full the locality notes accompanying specimens from the Kunene River and the Okavango delta (identifications inserted by the author).

M. J. Penrith (*in litt.* 11 May 1976) described the Kunene as a rather silt-laden river whos bed alternates between sand and rock. In sandy localities the channel is edged with *Phragmites*. Where rock is present it is either bare where the river is wide and slow-flowing (favourable *Etheria* habitats), or carpeted with *Hydrostachis* where it is fast flowing. There are fishes below the Ruacana Falls having affinities with rivers such as the Curoca and Quanza in Angola to the north.

At Ruacana B. F. Kensley collected four bivalve species from a single pool below the falls. His notes read: 'Hippo pool—small, muddy pool on Angolan side of river, bounded by sandy bar on the flowing river side and by reeds on the landward side. Maximum depth 0,9 m. Charophyte covering most of the bottom which consisted of a 2,5 cm layer of ooze, coarse sand below being black and anaerobic. *Caelatura kunenensis* most abundant, 6–10/m², in the ooze layer, *Mutela dubia* also lies (horizontally) in the first 2,5 cm of ooze. *Aspatharia pfeifferiana* and *A. wahlbergi* lay (vertically) about 7,6 cm below sand surface. *Mutela* and *Aspatharia* spp. were less common than *C. kunenensis*, seldom more than 1/m². Substrate surface scattered with dead shells, especially *C. kunenensis*. Openbill storks (*Anastomus lamelligerus* Temminck) observed feeding on bivalves. No water movement through pool and temperature higher than in flowing river.'

P. A. Reavell, who made a collection of bivalves near Maun in the Okavango delta, wrote: 'All specimens taken from the seasonally inundated area below perennial swamps. *Caelatura kunenensis* (typical form) prefers soft clay bottoms of streams in seasonally inundated area. Very common along Thamalakane River where in the dry season water may become stagnant with very low dissolved oxygen content. *Mutela dubia* usually together with *C. kunenensis* but more sporadic in distribution and of lower population density. *Aspatharia pfeifferiana* found only on clean, sandy bottoms where water was always flowing and dissolved oxygen content always high.' It is perhaps noteworthy that in many large *C. kunenensis* and *M. dubia* shells from the Thamalakane River erosion of the prismatic layer round the umbones and dorsal areas is unusually severe. This may be due to the action of aggressive carbon dioxide in the stagnant conditions which Reavell noted developed here.

These notes suggest that, while the bivalve species concerned are tolerant

of a wide range of dissolved oxygen concentration, *C. kunenensis* and *M. dubia* may prefer fine substrates such as clay and ooze whereas *Aspatharia* spp. may prefer coarser conditions.

Marshall (1975) found that in Lake MacIlwaine, a man-made impoundment on the Hunyani River in Rhodesia, *Mutela mabilli* (? = *M. dubia*) and *Caelatura mossambicensis* attained their greatest population densities ($31/m^2$ and $3/m^2$ respectively) and largest sizes in the riverine part of the lake. This was tentatively taken as evidence that these bivalves remain essentially riverine animals after impoundment, an interpretation in agreement with Fryer (1961) who found that the fish *Barbus altianalis radcliffi* was more heavily parasitized by larval *Mutela bourguignati* in the Victoria Nile than in Lake Victoria itself. This may have been due to the fish being more abundant in the riverine environment and therefore easier for the larvae to locate. If so, it suggests an important role for host fish in determining the distribution and population density of at least some Unionacea in lacustrine environments. This aspect is also discussed by Jubb (1976) who adds that *U. caffer* glochidia probably parasitize both truly fresh-water fish species and those which are capable of moving from fresh to saline water. Thus *U. caffer* could, when parasitic on fish of the latter type, i.e. the widespread *Sarotherodon mossambicus* (Peters), be carried from one river system to another via the sea, suggesting that spread of species from one drainage to another might be effected by processes other than geomorphic ones (river capture). He notes, too, that adult *U. caffer* are tolerant of salinities up to 3°/oo but not 5°/oo.

The large perennial Kunene, Okavango and Zambezi rivers rise on the southerly part of the central Angolan highlands at about 1 700 m altitude; the smaller Cuvelai River, more seasonal in character, rises on the southernmost spur of this plateau, the Serra Encoco. Over much of the drainage of these rivers the topography is very flat, with gradients of 1:30 000 or less. While the Kunene flows westwards to the Atlantic Ocean and the Zambezi eastwards to the Indian Ocean, the intervening area includes three endoreic or inland drainage systems, the Cuvelai/Ekuma/Etosha, the Cubango/Okavango/Ngami/Makari-kari and the Chobe/Liambezi/Linyanti. Where their beds are of sand or clay, these rivers broaden to create extensive floodplains where, in years of high rainfall, numerous low gradient valleys and channels (known in different areas as *oshanas*, *omurambas* or *mulapos*) become flooded and inundate vast areas of low-lying land. Water velocities in these seasonal watercourses seldom exceed 0,5 m/sec. (Stengel 1963: 375).

As far as a zoogeographical consideration of this malacofauna is possible, it is evident that the Kunene, Okavango and upper Zambezi River systems not only have several bivalve species in common but also constitute the southerly limits of the ranges of three west African Mutelidae, *Mutela dubia*, *Aspatharia pfeifferiana* and *Etheria elliptica*. Of the twelve unionacean species recorded from these systems the three Mutelidae listed above are predominantly west African species. Dartevelle (1939) attributed the similarity between the species

occurring in the upper Kunene and the Zambezi to capture of part of the drainage of the latter by the Kunene. *Caelatura kunenensis* is endemic to the western half of south-central Africa while *C. mossambicensis* and *Aspatharia petersi* are endemic to the eastern half. *Unio caffer* is a southern African endemic and *Aspatharia wahlbergi* enjoys a wide distribution in southern and east Africa. *Caelatura nyassaensis*, *C. hypsiprymna*, *Mutela alata* and *Aspatharia nyassaensis* are endemic to Lake Malawi.

Several examples exist of morphologically separable riverine and lacustrine forms of a species, e.g. *Caelatura kunenensis*, *Aspatharia wahlbergi* and *A. petersi*. Enough data are available to show (Fig. 3) that for *C. kunenensis* these differences are statistically significant (p < 0,01). This is probably a widespread phenomenon among freshwater Mollusca. Sutcliffe & Durrant (1977) have shown highly significant differences (p < 0,001) between the shell shapes of riverine and lacustrine populations of the limpet *Ancylus fluviatilis* (Muller) in England.

Similarities among the unionacean fauna of the river systems included in this study are probably due to connections between them during the Tertiary era (Gaigher & Mc. C. Pott 1973; Netterberg 1973) and to river capture. Connections still occur between the Okavango and upper Zambezi systems after exceptionally rainy seasons, when the waters of the Okavango flow via the Chobe/Linyanti rivers and the eastern Caprivi floodplain to the Zambezi at Kazungula, some 100 km upstream from the Victoria Falls. This floodplain is extremely flat, with a maximum height difference of only 20 m, so that in high flood the Zambezi may overflow in the reverse direction (Van der Waal 1974). Floods may occur more than once in each direction in a single rainy season.

Although the Kunene does not today overflow into Owambo even at high flood (Stengel 1963) there was before the breakthrough at the Ruacana Falls a previous connection with the Cuvelai/Etosha Pan system. Unfortunately, little bivalve material is available from this latter system. The upper tributaries to the Kunene, Okavango and Zambezi rivers not only lie close together, but their watersheds are ill-defined so that, in the dry seasons, it is difficult to tell in which direction they would flow (Wright 1963). Since these drainages were probably frequently connected during the pluvial periods of Pleistocene times, the spread of freshwater bivalves between them could readily occur. Fish might convey the parasitic stages of *C. kunenensis* and the Mutelidae from one drainage to another. Floods, too, can transport live bivalves. The author has found numerous large live *Unio caffer* scoured from the mud substratum of pools in a stream bed and carried by floods for considerable distances both downstream and away from its banks.

The apparent limits in the upstream distribution of *E. elliptica* in the Kunene River at the Ruacana Falls and of *C. mossambicensis* in the Zambezi at the Victoria Falls suggests that either large waterfalls or, since Ruacana is the most westerly of a series of falls, several smaller ones, may play important

roles in limiting bivalve distribution. This may be due to changes in substrate or to the barriers imposed by waterfalls on host fish distribution.

Except for *Caelatura mossambicensis*, and perhaps the little known *Aspatharia* (*A.*) *subreniformis* as well, the unionacean fauna of Lake Malawi consists of endemic forms with noticeably heavy shells (Mandahl-Barth 1972). This fauna seems to have affinities with the river systems to the west and south rather than with the other African Great Lakes to the north. Little is known of the Unionacea of the Shire River nor of how far south the Lake Malawi endemics are distributed within it. However, most occur in Lake Malombe as well and it is possible that the Murchison Falls (Shire River) act as a barrier here.

ACKNOWLEDGEMENTS

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